

Diving Physiology of Marine Mammals and Seabirds

Analyzing the physiological adaptations of marine mammals and seabirds, this book provides a comprehensive overview of what allows these species to overcome the challenges of diving to depth on a single breath of air. Through comparative reviews of texts on diving physiology and behavior from the last 75 years, Ponganis combines this research into one succinct volume.

Investigating the diving performance of marine mammals and seabirds, this book illustrates how physiological processes to extreme hypoxia and pressure are relevant to the advancement of our understanding of basic cellular processes and human pathologies. This book underscores the biomedical and ecological relevance of the anatomical, physiological, and molecular/biophysical adaptations of these animals to enable further research in this area.

An important resource for students and researchers, this text not only provides an essential overview of recent research in the field, but will also stimulate further research into the behavior and physiology of diving.

Paul J. Ponganis is a Research Marine Biologist and Marine Physiologist at the Scripps Institution of Oceanography, University of California, San Diego. A leading expert in the field and also an anesthesiologist, his primary clinical interests are in cardiac anesthesia, which he has practiced for the last 30 years in conjunction with his research at the Scripps Institution of Oceanography. His research has focused on the diving physiology of marine mammals and penguins at field sites around the world. In recognition of their Antarctic research, the Ponganis Icefall on Coulman Island was named after him and his wife.

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PAUL J. PONGANIS

Scripps Institution of Oceanography, University of California, San Diego



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To Katherine, my love and inspiration.

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Preface

The goal of this book is to provide students and researchers with a reference resource for the diving physiology of marine mammals and seabirds. To make progress in the future, it is essential to know what has been achieved in the past. It is my hope that this book will serve that purpose, and stimulate further research into both how these animals function in their environment and how their extreme adaptations may provide insight into basic physiology and pathophysiological processes.

It has been 25 years since the publication of Kooyman's *Diverse Divers*. Since that time, advances in biomedical technology and the advent of electronic backpack recorders have greatly expanded the field. Prior to that period, the pioneering work of Irving and Scholander in the 1930s and 1940s began the "modern" era of diving investigations. Consequently, more than 75 years of research, ranging from anatomical/physiological studies to biochemical/molecular investigations, are reviewed in this book. In my view, these topics are all parts of the animal's "physiology," and are relevant to the questions of both field biologists and laboratory investigators. In addition to future advances in electronic behavioral recorders, genomics, proteomics, and computer modeling, I want to encourage the development of physiological investigations to see how an animal functions and to determine what is actually happening within the body. To develop the tools and not interfere with natural behaviors is the challenge of the future.

As regards the book's layout, after initial chapters on diving behavior and the physiological challenges of diving, the chapters are primarily arranged along physiological themes, with a concluding chapter on biomedical applications. Cardiorespiratory physiology, oxygen store management, and hypoxemic/pressure tolerance receive the most emphasis, reflecting my primary interests.

I have tried to be as comprehensive as possible, but as with any book there will undoubtedly be newer papers published even as the book goes to press. In addition, if there are any significant publications omitted, especially in areas outside my expertise, I am responsible and attribute that to a lack of time and a demanding clinical schedule. Lastly, the inclusion of both marine mammals and seabirds into one book has necessitated division of many chapters into separate marine mammal and bird sections. As an aid to students, I have included the scientific name of a given species the first time it is used in every chapter as well as in each figure legend and table.

My perspectives on diving physiology stem from those of both a biologist and physician. I have been fortunate to be able to work as a biologist at Scripps Institution

of Oceanography as well as to have an active clinical practice in anesthesiology at Sharp Memorial Hospital in San Diego. It has been a unique experience: to collaborate with Jerry Kooyman, the foremost diving physiologist of my era, and to conduct an exciting clinical practice at what I consider has been San Diego's premier heart transplant and ventricular assist device center over the past 30 years. I still remember driving into the hospital the night we performed San Diego's first heart transplant in 1985.

To be able to pursue careers as both a biologist and anesthesiologist, I want to acknowledge K. S. Norris, my graduate student sponsor, and R. W. Pierce. Dick Pierce advised and supported my graduate work, taught the basics of diving physiology to two young Norris graduate students (D. Costa and myself), and was the force behind the scenes in the building of the UCSC Long Marine Lab. Similarly, my medical education and training at Stanford University were outstanding. And, of course, there is Jerry Kooyman, my long-time colleague and good friend at Scripps.

Much of my work has also benefited from the advice and assistance of SeaWorld's outstanding veterinary and animal care staff, and from consultations with Sam Ridgway, Red Howard, and the National Marine Mammal Foundation. What a luxury to have such expertise closely available. Anesthesia Service Medical Group has provided an outstanding clinical anesthesia practice opportunity with the flexibility to devote time to research and remote expeditions. My anesthesia partners and other physician colleagues at Sharp have been entirely supportive of this work. Again, I do not know of other medical practices in which such opportunities are available. To all, I am indebted.

I have also benefited from long-time associations and friendships with Roger Gentry, Phil Thorson, Mike Castellini, Randy Davis, Terrie Williams, Dan Costa, Markus Horning, Fritz Trillmich, Yvon Le Maho, Katsu Sato, Scott Eckert, Greg Marshall, Judy St. Leger, Tom Jue, and E. (Zhenya) Baranov. And in the era of microprocessor recorders, I cannot forget both my brother, Ed Ponganis, who developed our early electronic recorders in the 1980s, and the late Harve Hanish and his staff at UFI, who developed multiple custom physiological recorders for my more recent research. Many other collaborators have made significant contributions to my work including L. Winter, L. Welch, O. Matthieu-Costello, M. Costello, M. Scadeng, R. Spragg, D. Houser, T. Zenteno-Savin, S. Barber-Meyer, J. Heil, C. Champagne, H. Goforth, Y. Habara, and K. Shiomi. Lastly, there have also been my graduate students and fellows, all of whom have been outstanding, including P. Jobsis, D. Levenson, J. Meir, C. Williams, M. Tift, A. Wright, R. van Dam, T. Stockard, B. McDonald, J. Goldbogen, T. Welch, my US Navy anesthesia residents from Balboa Hospital, San Diego, and the many students Dan Costa allows me to "borrow" for field research.

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Lastly, I want to thank and acknowledge my collaborator and wife, Dr. Katherine V. Ponganis. It is she who has brought Jerry Kooyman and me kicking and screaming into the computer age. At the same time, she pursued research in cosmochemistry. It is

also her programming skills that have allowed us to decipher the reams of data collected by our physiological recorders. Many a graduate student has benefited from these programs. And she has had the patience and understanding to allow me to be both a biologist and physician, as well as to write this book.

Paul Ponganis MD, PhD
Scholander Hall
Center for Marine Biotechnology & Biomedicine, Scripps Institution of
Oceanography